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1 **Title: Do non-native plants affect terrestrial arthropods in the sub-Antarctic Kerguelen**

2 **Islands?**

3 Isabelle Badenhauer¹, Damien Fourcy², Mathilde Bertrand³, Aurélien Pierre³, Brigitte

4 Bonneau¹, Jean-Louis Chapuis⁴, Yann Rantier³, Maurice Hullé⁵

5 ¹ Unité de Recherche Pluridisciplinaire Prairies Plantes Fourragères, INRAE, F-86600

6 Lusignan, France.

7 ² UMR 0985, ESE, INRAE, Agrocampus Rennes, F-35042, Rennes, France.

8 ³ UMR 6553, ECOBIO, CNRS, Université Rennes 1, F-35000, Rennes, France.

9 ⁴ UMR 7204, CESCO, CNRS, Muséum National d'Histoire Naturelle, Université Pierre et
10 Marie Curie, Sorbonne Université, F-75005, Paris, France.

11 ⁵ UMR 1349, IGEPP, INRAE, Université Rennes 1, F-35653, Le Rheu, France.

12 * **Corresponding author:** Isabelle Badenhauer

13 **Tel: 0033(0)549556085**

14 email: isabelle.badenhausser@inrae.fr

15 ORCID: <https://orcid.org/0000-0002-6919-8647>

16

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24 The authors have no relevant financial or non-financial interests to disclose.

25

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27 The datasets generated and analysed during the current study are available in the Data INRAE
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29

30 **CODE AVAILABILITY**

31 Not applicable

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33 **AUTHORS' CONTRIBUTIONS**

34 IB and MH conceived and designed research. IB, MB, AP conducted experiments. IB and BB
35 identified arthropods. DF developed analytical tools to analyse Pléiades images and produced
36 vegetation maps. YR designed geostatistical application for fieldwork. JLC provided long-term
37 plant database. IB analysed data. IB and MH wrote the manuscript. DF and JLC commented on
38 previous versions of the manuscript. All authors read and approved the final manuscript.

39

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41 Not applicable

42

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44 Authors obtained all the appropriate permissions for collecting arthropods in the “Réserve
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54 **ABSTRACT**

55 Biological invasions are a major threat to the terrestrial ecosystems of the sub-Antarctic islands.
56 While non-native plants generally have negative impacts on native arthropods, few studies have
57 investigated how both native and non-native arthropods and plants interact in the sub-Antarctic
58 islands. This was the aim of our study, which was conducted on three islands of the Kerguelen
59 archipelago. The design was based on the spatial proximity of areas dominated by non-native
60 or native plant species. Trait-based indices were calculated to characterize the functional
61 structure of plant communities, considering plant stature and leaf traits. Native and non-native
62 vegetation had contrasting functional composition but their functional diversity was similar.
63 The effects of the type of vegetation, native or non-native, and plant functional diversity on
64 arthropods were tested. Native macro-arthropod richness and abundance were similar or higher
65 in non-native vegetation, and benefited from greater plant functional diversity. Abundances of
66 macro-herbivores, macro-decomposers and macro-predators were also similar or higher in non-
67 native vegetation. Conversely, the abundances of micro-arthropods, Symphypleona springtails
68 and Oribatida mites, were higher in native vegetation but we also found that plant functional
69 diversity had a negative effect on Symphypleona. Our results suggest that non-native plants can
70 affect micro-arthropods directly or indirectly, likely through their effects on abiotic factors. By
71 affecting macro-arthropod abundances across different trophic groups and by depleting micro-
72 arthropods, non-native plants can alter trophic interactions, functional balances and the
73 functioning of whole ecosystem.

74

75 **Keywords**

76 Biodiversity; biological invasions; species richness; vascular plants; functional traits

77

78

79 **INTRODUCTION**

80 The Kerguelen Islands are located in the South Indian Ocean, and include a main island of 6675
81 km² and about sixty other islands (1 km²-200 km²) (Fig 1). Like the other sub-Antarctic islands,
82 their terrestrial ecosystems are characterized by strong geographical and historical isolation.
83 They harbor a small number of sub-Antarctic species for both flora and fauna due to low levels
84 of immigration from nearby continents and harsh environmental conditions (Chown et al.
85 1998). Terrestrial ecosystems are very simple, natively lacking some taxonomic groups such as
86 mammals, amphibians and reptiles. Low plant diversity at the species and botanical family
87 levels characterizes the native flora, which is composed of 29 species of vascular plants (Frenot
88 et al. 2001). Native macro-arthropod communities are composed of 22 native insect species and
89 two native spider species (Hullé and Vernon 2021), while micro-arthropod communities which
90 are dominated by Oribatida mites and springtails are respectively composed of 24 and 18 native
91 species (Deharveng and Travé 1981). It should be noted that micro-arthropod diversity may be
92 underestimated and that some ‘undiscovered’ or cryptic species are likely to be found using
93 recent advances in molecular biology in Antarctic (Collins et al. 2020). Macro-arthropod
94 communities are unbalanced, some trophic groups being absent or not abundant such as
95 herbivores, pollinators and decomposers such as flies dominate macro-arthropod communities
96 due to the large amounts of marine mammal and seabird excretions (Chown and Convey 2016).
97 Despite the geographical isolation of the Kerguelen Islands, many species among plants,
98 arthropods and mammals have been introduced, voluntarily or involuntarily, due to human
99 activities, and have established. For instance, there are currently as many non-native as native
100 macro-arthropod species (Hullé and Vernon 2021), while few non-native micro-arthropod
101 species have been recorded (Deharveng and Travé 1981; Greenslade and Convey 2012). For
102 plants, the number of species in some sites historically frequented by humans has become three

103 times greater than the number of native species (Frenot et al. 2005), having potentially
104 important impacts on ecosystem processes.

105 Biological invasions are widely recognized as being one of the most significant threats
106 to biodiversity and are expected to increase with global warming (Shaw et al. 2010; McGeoch
107 et al. 2015). Sub-Antarctic islands are deeply affected by climate change (Lebouvier et al. 2011)
108 which makes their ecosystems more suitable to less stress-adapted non-native species (Pertierra
109 et al. 2017). In addition, some established non-native species may become invasive (Frenot et
110 al. 2005), exacerbating their impact on biodiversity and ecosystems due to the disruption of
111 interaction networks (Dunn and Hatcher 2015). In general, invasive plants reduce the diversity
112 of native plant species and are predicted to also negatively impact native arthropod diversity
113 (review in Spafford et al. 2013) through different mechanisms such as the alteration of
114 vegetation structure or the loss of some plant species which host specialist arthropods. Few
115 native specialist arthropods are present on the Kerguelen Islands, e.g., the moth *Embryonopsis*
116 *halticella* which feeds on *Poa cooki* (Crafford and Scholtz 1986), and the fly *Calycopteryx*
117 *moseleyi* (Tréhen et al. 1986), the weevils *Bothrometopus angusticollis* and *Canonopsis sericea*
118 which feed on *Pringlea antiscorbutica* (Voisin et al. 2017), and the loss of their host-plant might
119 particularly affect them.

120 Arthropods are highly dependent on plants (Schaffers et al. 2008; Joern and Laws 2013)
121 and different components of plant community features affect them, such as plant composition,
122 or morphological and physical attributes. For instance, plant height and lateral spread as well
123 as leaf dimensions characterize plant architecture and determine the availability of different
124 micro-habitat conditions allowing or not arthropods to choose optimal conditions of
125 temperature, protection against wind, rain or predators (Spafford et al. 2013; Gardarin et al.
126 2018). By providing attachment points for spider webs, architectural traits may have an impact
127 on predator hunting efficacy, depending on predator hunting strategy and on predator-prey

128 interactions (Pearson 2009). Vegetation stature also influences the distribution of soil-dwelling
129 arthropods likely through its correlation with litter quantity (Gardarin et al. 2018). For
130 herbivores, which have direct interactions with plants since they feed on them, Carmona et al.
131 (2011) showed that morphological and physical plant traits may act as a physical barrier and
132 are often more important for plant-herbivore interactions than chemical traits. For instance,
133 traits related to the biomechanical properties, such as cuticle thickness, specific leaf area
134 (Ordonez et al. 2010), or leaf dry matter content (Deraison et al. 2015) have been shown to
135 impact herbivore choice when selecting their food plant.

136 How arthropod communities reliant on native vegetation on sub-Antarctic islands, are
137 impacted by non-native plants is yet to be tested (Houghton et al. 2019) and is difficult to
138 predict. This is due to the absence or low richness of many insect groups (Gressitt 1970; Vernon
139 et al. 1998), and to the high interactions at play between native and non-native plants, native
140 and non-native arthropods and between plants and arthropods (Houghton et al. 2019). Trait-
141 based approaches have been proposed as useful tools to study plant-arthropod interactions at
142 the community level (Lavorel et al. 2013; e.g., Deraison et al. 2015; Le Provost et al. 2017) and
143 to understand community responses to biotic disturbance induced by non-native species (Gross
144 et al. 2013; Mouillot et al. 2013). This study aimed to investigate the effects of plant
145 communities dominated by native or non-native plant species on macro- and micro-arthropod
146 communities on three islands of the Kerguelen archipelago. On each of the studied islands, we
147 selected relatively large areas of the two types of vegetation, i.e., native and non-native, that
148 were close to each other. By considering plant traits involved in plant-arthropod interactions,
149 i.e., plant architecture and leaf attributes, we assessed whether the plant functional community
150 structure differed between the two types of vegetation using complementary indices, the
151 functional dispersion and the community-weighted mean of traits (Mouillot et al. 2013).
152 Secondly, we estimated the taxonomic diversity of macro-arthropods and their abundances as

153 well as the abundances of epigaeic micro-arthropods in both types of vegetation. We then
154 investigated whether these components of arthropod communities differed between native and
155 non-native plant communities and whether plant functional diversity and community-weighted
156 means of traits explained a significant part of their variability.

157

158 MATERIAL AND METHODS

159 STUDY AREA AND SAMPLING DESIGN

160 The study was conducted during the summer 2017-2018 on three islands of the *Golfe du*
161 *Morbihan* in the Kerguelen archipelago (48° 30'–50° S, 68° 27'–70° 35' E): *Île Australia*, *Île*
162 *aux Cochons* and *Île Mayes* (Fig. 1). Originally, plant communities were dominated by *Acaena*
163 *magellanica*, *Azorella selago*, *Festuca contracta* and *P. antiscorbutica*. These plant assemblies
164 covered *Île Australia* and *Île Mayes* until the 2010s. From these years, following climate
165 change, non-native Poaceae and Asteraceae developed, in particular *Poa pratensis* and
166 *Taraxacum gr. ruderalis*. These plants have expanded widely on *Île Mayes*, where meadows of
167 *P. pratensis* covered large areas in 2016. On *Île Australia*, non-native Poaceae communities (*P.*
168 *pratensis*, *Vulpia bromoides*) were still localized in 2016. *Île aux Cochons* differed from the
169 other two islands by the presence of rabbits (*Oryctolagus cuniculus*) until 1997, when they were
170 eradicated (Chapuis et al. 2001). This mammal resulted in the rarefaction of *P. antiscorbutica*
171 and *A. selago*, replaced by *A. magellanica*, which covered more than 90% of the island in 1997
172 (Chapuis et al. 2001; Chapuis et al. 2002). During the years 2000-2010, the increase in
173 temperature and especially the low summer precipitations (Lebouvier et al. 2011) resulted in
174 the significant regression of *A. magellanica* and the development of non-native Asteraceae
175 (*Taraxacum erythrospermum*, *T. gr. ruderalia*) and Poaceae (in particular *P. pratensis*).
176 Currently, the communities dominated by native species, i.e., *A. magellanica*, occupy small

177 areas. All three islands have been colonized by mice, which have heavily predated and damaged
178 their invertebrate fauna (Chapuis et al. 2002).

179 The sampling design consisted of areas of native- or non-native-dominated vegetation
180 that were close to each other (a few tens of meters). It was implemented in herbaceous habitats
181 which are the main habitats colonized by non-native plants. Sites corresponding to these criteria
182 were preselected using a remote sensing based cartography of the vegetation on the three
183 studied islands (Fourcy et al. 2018) (Fig. 2; see Online Resource 1 for a complete description
184 of the classes). Vegetation maps were produced from a multispectral Pléiades image acquired
185 in February 2016 (2 m ground spatial resolution) that we analysed by performing a supervised
186 classification with machine-learning algorithms. The supervised classification was based on
187 botanical surveys conducted in December 2016 on training zones on *Île Australia*, *Île aux*
188 *cochons* and *Île Mayes*, and used as references for the machine-learning algorithms.

189 Within each island, we selected in the field five sites among the preselected sites where
190 an area covered with >90% of native plant species was close to an area covered with >90% of
191 non-native plant species. The percent coverage of vegetation was estimated visually at that step.
192 Then, we delineated a patch >150 m² within each of these areas and surveys were carried out
193 within each patch. Distance between the two types of patch within a site ranged from 15 m to
194 58 m. This resulted in 30 vegetation patches: 3 islands, 5 sites per island, 2 patches per site (one
195 non-native, hereafter “non-native patch”, and one native, hereafter “native patch”) (Fig. 2).
196 When selecting the sites, we controlled for abiotic conditions known to affect arthropods, such
197 as the altitude, distance from the sea (Hullé and Vernon 2021), slope, dominant wind and sun
198 exposures. All sites were at < 40 m altitude, > 50 m from the sea, with a slope <20%. Sun and
199 dominant wind exposures differed between sites and islands but not between paired patches
200 (Online Resource 2).

201 Note that the sampling conditions varied during the study. Harsh weather conditions
202 were observed in *Île aux Cochons* where a hailstorm occurred during one day and in *Île Mayes*
203 where low temperatures (4.4°C on average) and snowstorm occurred during three days.
204 Conversely, sunny weather conditions were recorded throughout the sampling period in *Île*
205 *Australia*.

206

207 PLANT SURVEYS AND TRAITS

208 A botanical survey was conducted within each of the 30 patches on the first day of the
209 experiment (20th December 2017 on *Île aux Cochons*, 29th December 2017 on *Île Australia*, 9th
210 January 2018 on *Île Mayes*). We used five quadrats of 0.50 m x 0.50 m haphazardly located
211 within each patch. In each quadrat, we recorded the number of plant species and we estimated
212 a percentage cover of the quadrat surface for each plant species. We calculated plant species
213 diversity and mean cover of each plant species per patch over the five quadrats.

214 To characterize plant community features, seven plant traits reflecting important
215 functions for plants (Diaz et al. 2016), and involved in plant-arthropod interactions (Carmona
216 et al. 2011; Gardarin et al. 2018) were selected: plant height (PH) and plant width (PW), leaf
217 length (LL) and leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), and
218 leaf thickness (LT). In each island, 15-30 specimens of each plant species covering >10% of at
219 least one vegetation patch were measured and one leaf per plant was sampled, excepting *A.*
220 *selago* and *P. antiscorbutica* for which we only sampled a total of 2-5 leaves. Traits were
221 measured following standard protocols (Cornelissen et al. 2003) and their values were averaged
222 over the number of plant or leaf specimens per plant species and island.

223

224 ARTHROPOD SAMPLING

225 On the first or second day of the experiment, we sampled arthropods in the 30 patches (one
226 trapping session) using two types of trap to accurately estimate arthropod diversity: pitfall traps
227 and yellow pans (Southwood 1978). We placed five pitfall traps (7.5 cm diameter, 5 cm depth)
228 and two yellow pans (20 cm diameter) per patch. Pitfall traps were placed haphazardly in the
229 patch, while yellow pans were placed on the ground and located so that the distance was the
230 highest between the native patch and the non-native patch within each site. Traps were filled
231 with a preservative solution of water, a few drops of liquid soap and salt (10 gL⁻¹). All traps
232 within an island were set up on the same day and left in place for four trapping days. We stored
233 all caught arthropods in the lab in a 70% ethanol solution. Macro-arthropods were identified to
234 the lowest possible taxonomic level (usually species) following Hullé et al. (2018). We
235 identified winged aphids to species level while we pooled all wingless aphids together.

236 We characterized macro-arthropods, i.e., insects and spiders, by calculating their
237 taxonomic richness and abundance. For this purpose, we defined different groups of macro-
238 arthropods according to their origin status and trophic group according to Hullé and Vernon
239 (2021). To calculate taxa richness, we first pooled for each patch all macro-arthropods collected
240 either in pitfall traps or in yellow pans. Then, we calculated native, non-native and total taxa
241 richness, which included taxa with unknown native or non-native status. We also calculated
242 taxa richness of three trophic groups: decomposers (taxa feeding on plant material and
243 omnivorous taxa), herbivores and predators. For macro-arthropod abundances, we considered
244 native macro-arthropods and performed separate analyses for pitfall traps and for yellow pans,
245 pooling all individuals sampled in each patch. We also analysed the abundances of decomposers
246 in yellow pans, herbivores in yellow pans and predators in pan traps by pooling all individuals
247 sampled in each patch (see Badenhauer (2021) for a complete description of dataset). For
248 micro-arthropods, we focussed on the abundances of Oribatida mites and Symphypleona
249 springtails, which are generally epigaeic and tend to occur above or on the top of the ground

250 surface (Greenslade 2002). We analysed their abundances in pitfall traps by pooling all
251 individuals sampled in each patch.

252

253 STATISTICAL ANALYSES

254 All statistical analyses were performed using the R statistical software (R Development Core
255 Team 2020) version 4.0.3 and packages car (Fox and Weisberg 2019), emmeans (Lenth 2020),
256 factoextra (Kassambara and Mundt 2020), FactoMineR (Le et al. 2008), FD (Laliberté and
257 Legendre 2010; Laliberté et al. 2014) and lme4 (Bates et al. 2015).

258

259 *Characterization of plant functional community structure*

260 Two complementary components of the functional structure of plant communities were
261 assessed, i.e., functional composition and functional diversity (Laliberté and Legendre 2010;
262 Mouillot et al. 2013). Plant functional composition was estimated using the community
263 weighted mean index calculated for each trait, CWM , and functional diversity using the multi-
264 trait functional dispersion index, $FDis$. Both indices were calculated following Laliberté and
265 Legendre (2010).

266 CWM is the mean trait value of the community, weighted by the relative cover of each
267 plant species. It reflects the trait values of the dominant species in the community. It was
268 computed separately for the seven measured traits (CWM_{TRAIT}):

$$269 \quad CWM_{TRAIT} = \sum_{j=1}^n p_j T_j$$

270 where n is the number of plant species in the vegetation patch, p_j is the relative cover of species
271 j in the patch (mean of species cover over the five quadrats per patch), and T_j is its mean trait
272 value per island.

273 *FDis* is the mean distance in multidimensional trait space of individual species to the
274 centroid of all species. It takes into account species abundances weighting distances of
275 individual species by their relative abundances. Its minimum value is 0, when the community
276 is composed of only one species. High *FDis* value in plant communities reflects a strong
277 disparity in the distribution of traits. By providing a greater number of niches and microhabitats
278 for arthropods, high *FDis* is expected to result in greater arthropod diversity (e.g., Deraison et
279 al. 2015). It was computed as:

$$280 \quad FDis = \frac{\sum_{j=1}^n a_j z_j}{\sum_{j=1}^n a_j}$$

281 where n is the number of plant species in the vegetation patch, a_j is the cover of species j in the
282 patch (mean of species cover over the five quadrats per patch), z_j is the distance of species j to
283 the weighted centroid of the $[x_{ij}]$ (trait \times species) matrix, c :

$$284 \quad c = [c_i] = \frac{\sum_{j=1}^n a_j x_{ij}}{\sum_{j=1}^n a_j}$$

285 We performed a principal component analysis (PCA) on the CWM_{TRAIT} of the seven
286 selected traits to describe plant community features in the two types of patch and to evaluate
287 how they correlated.

288 We used Linear Mixed Effects Models (LMM) fitted by log-likelihood criterion to test
289 for the effect of the island and type of patch on plant species richness, the seven CWM_{TRAIT} and
290 *FDis*. The interaction term between the type of patch and the island was included in the models
291 since the effect of non-native plants may depend on the island and its invasion history. The site
292 was included in the models as random effect to take into account for the effects of similar abiotic
293 environmental conditions in the two patches per site. Models were simplified step by step by
294 removing the interaction term and the main fixed effects if not significant ($\alpha = 0.05$) using Wald
295 Chi-square test, χ^2 . Parameters of the final models were estimated using restricted maximum
296 likelihood (REML), and least-squares means were calculated. Predicted means were compared

297 using Tukey method and adequate contrasts. Model errors were inspected for normality,
298 constant mean and variance. Model formula was:

$$299 \quad Y \sim (1|Site) + Island * Type\ of\ patch$$

300

301 *Effects of plant communities on arthropod communities*

302 The effects of plant communities on the richness and abundance of arthropods were analysed
303 using LMM or Generalized Linear Mixed Effects Models (GLMM) depending on the
304 distribution of the data and model errors, in order to satisfy the statistical assumptions of
305 models. LMM was used for analysing i/ the taxa richness of macro-arthropods: native species,
306 non-native taxa (sqrt-transformed), all taxa (sqrt-transformed), decomposers (sqrt-
307 transformed), herbivores and predators; ii/ the abundances of macro-arthropods: decomposers
308 (log-transformed), herbivores (log-transformed), predators (log-transformed); iii/ the
309 abundance of Oribatida mites (log-transformed). GLMM with Poisson errors was used for
310 analysing i/ the abundance of native macro-arthropods and ii/ the abundance of Symphypleona
311 springtails.

312 First, we tested for the effects of the type of patch and plant *FDis* on the response
313 variables mentioned above. We included in the models the island, the type of patch and their
314 two-way interaction, and plant *FDis* as fixed effects. The site was included as random effect in
315 all models. The model had the following structure:

$$316 \quad Y \sim (1|Site) + Island * Type\ of\ patch + FDis$$

317 Model simplification was conducted firstly by removing non-significant interaction
318 term. Statistical assumptions were inspected, and model predictions and mean comparisons
319 were performed as described above.

320 Second, we aimed to establish the relative importance of the functional composition of
321 plant communities, namely *CWM_{TRAITs}* and other components of plant community such as plant

322 species identity, in shaping arthropod communities. However, collinearity issues occurred when
323 including the type of patch and single CWM_{TRAITs} in the same statistical models because
324 CWM_{TRAITs} and the type of patch were highly correlated (VIF values >2) (Zuur et al. 2010). For
325 this reason and as an exploratory analysis, we have limited the analysis of the effects of
326 CWM_{TRAITs} on arthropods to a comparison of models including either the type of patch or single
327 CWM_{TRAITs} . As described above, we run LMM or GLMM to model macro-arthropod taxa
328 richness and abundances, and micro-arthropod abundances. Model formula for the patch model
329 was:

$$330 \quad Y \sim (1|Site) + Island * Type\ of\ patch$$

331 Model formula for the CWM_{TRAIT} models was:

$$332 \quad Y \sim (1|Site) + Island * CWM_{TRAIT}$$

333 After model simplification as described above, an information-theoretic approach (AIC-
334 based approach corrected for small sample size; $AICc$; Burnham and Anderson 2002) was used
335 to compare for each CWM_{TRAIT} the simplified patch model and CWM_{TRAIT} model. $AICc$
336 difference (delta $AICc$) between the two models was calculated. If $|\text{delta } AICc| < 2$, models were
337 not significantly different, while if $|\text{delta } AICc| > 2$ they differed, the best model being the one
338 with the smallest $AICc$.

339

340 RESULTS

341 CHARACTERIZATION OF PLANT COMMUNITIES AT THE PATCH SCALE

342 Main native plant species in the patches were *A. magellanica*, *A. selago*, *F. contracta*, and *P.*
343 *antiscorbutica* and main non-native species were *P. pratensis* generally associated with *T. gr.*
344 *ruderalia*, and *T. erythrospermum*. Non-native plant species covered on average >95% in non-
345 native patches (Fig. 3d, e, f) while native plant species covered ~ 90% in native patches (Fig.
346 3a, b, c). Total plant species richness per patch did not vary between native and non-native

347 patches (LMM: $p (>\chi^2_1) = 0.1484$). It was significantly lower (LMM: $p (>\chi^2) = 0.0230$) on *Île*
348 *Australia* (estimated mean $\pm SE$, 3.1 ± 0.6 plant species) and *Île Mayes* (3.4 ± 0.6) than on *Île*
349 *aux Cochons* (5.3 ± 0.8). These differences between islands were due to differences in non-
350 native plant species richness in the native patches, which was higher on *Île aux Cochons* than
351 on *Île Mayes* than on *Île Australia* (LMM: Island: $p (>\chi^2) = 0.0001$; Type of patch: $p (>\chi^2) =$
352 0.0030 ; Island \times type of patch: $p (>\chi^2) = 0.0321$). Native plant species richness was the same in
353 both types of patch and on the three islands (observed mean $\pm SE = 1.9 \pm 0.3$). The functional
354 dispersion $FDis$ did not vary between the types of patch but between islands (Table 1).

355 The PCA performed on CWM_{TRAITS} showed that non-native and native patches formed
356 distinct groups in the space of the two first PCA axes which accounted for 82.9% of the variance
357 (Online Resource 3). The first PCA axis (60.1% of explained variance) mainly correlated to
358 leaf dimensions, i.e., leaf length (CWM_{LL}) ($r = 0.96$) and leaf area (CWM_{LA}) ($r = 0.86$). The
359 second PCA axis (22.8% of explained variance) correlated to leaf thickness (CWM_{LT}) ($r =$
360 0.79).

361 All CWM_{TRAIT} values differed significantly between native and non-native patches
362 (Table 1). Native patches were characterized by low-stature plants, thick and small leaves, small
363 SLA, and large LDMC. Non-native patches were characterized by large stature plants (+33%
364 CWM_{PH} ; +36% CWM_{PW}), thinner leaves (-45% CWM_{LT}) with larger dimensions (+103% CWM_{LL} ;
365 +80% CWM_{LA}), larger SLA (+38% CWM_{SLA}) and smaller LDMC (-15% CWM_{LDMC}). All
366 CWM_{TRAIT} values but CWM_{SLA} also differed between islands (Table 1).

367

368 EFFECTS OF PLANT COMMUNITIES ON MACRO-ARTHROPOD COMMUNITIES

369 Overall, we collected nine native macro-arthropod species, 16 non-native taxa (among which
370 13 species), and four taxa not classifiable as native vs non-native species (*Smittia* sp., *Ixodes*
371 spp., Siphonaptera, Thysanoptera). Among macro-arthropods, 785 of the collected individuals

372 belonged to native species (560 in pitfall traps, 225 in yellow pans), 49 224 to non-native taxa
373 and 108 specimens were not classifiable (70 *Smittia* sp., 36 Siphonaptera, one *Ixodes* spp., one
374 Thysanoptera). One non-native taxa was numerically dominant, i.e., the aphids which
375 represented >90% of the total counts whatever the type of patch and island (see Badenhäusser
376 (2021) for a complete description of dataset).

377

378 *Macro-arthropod diversity and native macro-arthropod abundance*

379 The same native macro-arthropod species with very few exceptions were collected in native
380 and non-native patches within each island. They belonged to three trophic groups, i.e.,
381 decomposers, herbivores and predators. Taxa richness of native macro-arthropods was low and
382 differed between islands (estimated means \pm SE, *Île Australia*: 3.5 ± 0.4 ; *Île aux Cochons*: 2.7
383 ± 0.4 ; *Île Mayes*: 1.9 ± 0.4) (Table 2). The type of patch had no effect on the taxa richness of
384 native macro-arthropods but plant *FDis* had a positive significant effect (Table 2) (LMM:
385 Parameter estimate \pm SE, 6.31 ± 3.11) suggesting that a wide variety of food niches or micro-
386 habitats was favorable to native macro-arthropods. Taxa richness of non-native macro-
387 arthropods was roughly twice the taxa richness of native macro-arthropods and differed
388 between islands (*Île Australia*: 7.6 ± 0.7 ; *Île aux Cochons*: 5.1 ± 0.6 ; *Île Mayes*: 4.3 ± 0.5)
389 (Table 2). The type of patch and *FDis* had no effect on the taxa richness of non-native macro-
390 arthropods (Table 2). Total macro-arthropod richness per patch was the same in native and non-
391 native patches on *Île Australia* (native patches: 11.9 ± 1.3 ; non-native patches: 13.7 ± 1.3) and
392 *Île aux Cochons* (native patches: 9.2 ± 1.0 ; non-native patches: 7.6 ± 1.0) (Table 2). On *Île*
393 *Mayes*, it was significantly lower in native patches (5.2 ± 0.8) relative to non-native patches
394 (8.2 ± 1.0) (Table 2). *FDis* had a positive significant effect on total richness (Table 2).

395 The native spiders, *Neomaso antarcticus* and *Myro kerguelensis*, represented ~90% of
396 the abundances of native macro-arthropods collected in pitfall traps whatever the type of patch

397 and the island, and >50% in yellow pans. Native macro-arthropod abundances in pitfall traps
398 were significantly lower in native patches relative to non-native patches and differed between
399 islands (Table 2, Fig. 4a). In addition, they increased significantly with *FDis* (Table 2) (GLMM:
400 Parameter estimate \pm *SE*, 2.46 ± 1.09). The island, type of patch, and *FDis* had no significant
401 effect on the abundances of native macro-arthropods collected in yellow pans (GLMM: Island:
402 $p (>\chi^2) = 0.0966$; Type of patch: $p (>\chi^2) = 0.9381$; Island \times Type of patch: $p (>\chi^2) = 0.2201$;
403 *FDis*: $p (>\chi^2) = 0.1413$).

404 Results of the comparison between the patch model and *CWM_{TRAIT}* models showed that
405 *CWM_{PW}* and *CWM_{LA}* models were better than the patch model in explaining the taxa richness
406 of native macro-arthropods (Online Resource 4). In these models, *CWM_{PW}* and *CWM_{LA}* had
407 opposite effects depending on the island (Online Resource 4). No *CWM_{TRAIT}* model was selected
408 as the best model relative to the patch model in explaining the non-native and total taxa richness,
409 and the abundance of native species (Online Resource 4).

410

411 *Diversity and abundance of trophic groups*

412 Herbivores represented >95% of the counts whatever the island and type of patch
413 (Online Resource 5). This group was mainly composed of four aphid species among which
414 *Myzus ascalonicus* was dominant (>95% of winged aphids), and one thrips species *Apterothrips*
415 *apteris*. Four native species represented other herbivores, which were very few (47 individuals
416 in total). Singular fit occurred in LMM conducted on herbivore richness, which was not
417 analysed. Herbivore abundance was similar or higher depending on the island in non-native
418 patches relative to native (Table 2; Fig. 4b). Plant *FDis* had strong effects on herbivore
419 abundance, which increased with increasing *FDis* (Table 2) (LMM: Parameter estimate \pm *SE*,
420 11.22 ± 3.58). In addition, *CWM_{LL}* and *CWM_{SLA}* models explained significantly more variability
421 in herbivore abundance relative to the patch model (Online Resource 4). Herbivore abundance

422 increased with increasing CWM_{LL} and CWM_{SLA} whose single effects were selected in the
423 simplified models (Online Resource 4).

424 Decomposers (feeding on plant material and omnivorous pooled) represented ~1% of
425 the macro-arthropods (Online Resource 5). This group was the richest with 13 taxa, among
426 which the sciarid *Lycoriella sativae* represented half of the counts. Decomposer taxa richness
427 was the same in both types of patch on *Île Australia* (estimated means $\pm SE$, native patches: 4.4
428 ± 0.8 , non-native patches: 5.1 ± 0.9), and *Île aux cochons* (native patches: 3.2 ± 0.7 , non-native
429 patches: 2.4 ± 0.6). It was higher in non-native patches relative to native patches on *Île Mayes*
430 (native patches: 1.7 ± 0.5 , non-native patches: 3.0 ± 0.7) (Table 2). The same results were
431 observed for decomposer abundance (Table 2, Fig. 4c). $FDis$ had no effect on decomposer taxa
432 richness and abundance (Table 2). CWM_{LA} and CWM_{LDMC} models better modeled decomposer
433 taxa richness than the patch model, and the effects of CWM_{LA} and CWM_{LDMC} differed between
434 islands (Online Resource 4).

435 Predators represented 2.6% of the macro-arthropods collected in pitfall traps (Online
436 Resource 5). Predator trophic group was composed of two native spider species, *N. antarcticus*,
437 *M. kerguelensis*, and two non-native species, the spider *Tenuiphantes tenuis*, and the carabid
438 beetle, *Merizodus soledadinus* (only 2.0% of the predators). Predator richness was the same in
439 native and non-native patches on *Île Australia* (native patches: 3.0 ± 0.3 ; non-native patches:
440 3.4 ± 0.3) and on *Île Mayes* (native patches: 2.2 ± 0.3 ; non-native patches: 2.6 ± 0.3). On *Île*
441 *aux Cochons* it was higher in native patches (3.2 ± 0.3) than in non-native patches (2.6 ± 0.3)
442 (Table 2). Predators were significantly more abundant in non-native patches relative to native
443 ones on *Île Australia* and *Île Mayes* (Table 2, Fig. 4d). On *Île aux Cochons*, they were as
444 numerous in both types of patch (Table 2, Fig. 4d). Neither $FDis$ nor CWM_{TRAITS} had any effect
445 on predator richness and abundance (Table 2, Online Resource 4).

446

447 EFFECTS OF PLANT COMMUNITIES ON MICRO-ARTHROPOD COMMUNITIES

448 Overall, 9845 micro-arthropods were collected in pitfall traps among which 9001 Oribatida
449 mites and 844 Symphypleona springtails. Oribatida mites represented >80% of micro-
450 arthropods on the three islands. Native patches had higher Oribatida mite (Fig. 5a) and
451 Symphypleona springtail (Fig. 5b) abundances relative to non-native patches whatever the
452 island (Table 2). *FDIs* had a strong negative effect on Symphypleona springtails (GLMM:
453 Parameter estimate \pm SE, -7.25 ± 1.00) while it had no effect on Oribatida mites (Table 2).
454 Results of the comparison between the patch model and *CWM_{TRAITS}* models showed that
455 *CWM_{PW}* model was better than the patch model in explaining Symphypleona abundance, which
456 decreased with increasing *CWM_{PW}* whatever the island (Online Resource 4).

457

458 DISCUSSION

459 Our study shows opposite effects of non-native plants on macro-arthropods and micro-
460 arthropods. Despite strong differences in the functional composition of plant communities, we
461 didn't demonstrate any negative effect of non-native plants on native macro-arthropods. In fact,
462 macro-arthropod diversity and abundance were similar or higher in non-native plant
463 communities whatever their native or non-native status, and their trophic group. Conversely,
464 micro-arthropods, i.e., Symphypleona springtails and Oribatida mites, abundances were higher
465 in native plant communities relative to non-native. Finally, we found that plant functional
466 diversity was similar in native and non-native plant communities, and benefited native macro-
467 arthropods while it had a null or negative effect on micro-arthropods.

468

469 FUNCTIONAL STRUCTURE OF NATIVE AND NON-NATIVE PLANT COMMUNITIES

470 Trait-based indices, i.e., *CWM_{TRAITS}* and *FDIs*, were used to characterize the functional
471 composition and diversity of native and non-native patches. Traits associated with leaf structure

472 and quality were expected to be involved in trophic plant-arthropod interactions, and those with
473 plant stature in non-trophic interactions through their effects on arthropod habitats (Lavorel et
474 al. 2013; Gardarin et al. 2018). All CWM_{TRAITS} differed between the two types of patch,
475 reflecting the very high cover of respectively native and non-native plant species in the patches
476 and trait differences between dominant native and non-native species. Dominant native plant
477 species, i.e., *A. magellanica* and *F. contracta*, had low stature and leaf dimensions, low SLA
478 and high LDMC, indicating low relative growth rate, low nutrient content and slow resource
479 capture. They contrasted with dominant non-native species, i.e., *P. pratensis* and *T. gr.*
480 *ruderalia* whose large stature and leaf dimensions, large SLA and low LDMC, correspond to
481 fast-growth rate, high nutrient content and good light competitor (Diaz et al. 2016). Other
482 studies also observed these characteristics in native and non-native plant communities
483 (Ordonez et al. 2010; Gross et al. 2013). We also found that $FDIs$ did not differ between native
484 and non-native patches. This reflects the fact that native and non-native species did not mix or
485 mixed very little within the patches. It also reflects similar range of trait disparity between the
486 two dominant species within each type of patch, i.e., between a grass species (*F. contracta* in
487 native patches and *P. pratensis* in non-native patches) and an herb species (*A. magellanica* in
488 native patches and *T. gr ruderalia* in non-native patches).

489

490 NON-NATIVE PLANTS HAVE NO NEGATIVE EFFECT ON NATIVE MACRO- 491 ARTHROPODS

492 Plant $FDIs$ significantly contributed to explaining the effect of plants on native macro-
493 arthropods, which benefited as expected from a greater diversity of plant resources and micro-
494 habitats in both native and non-native vegetation. Differences in the composition of native and
495 non-native vegetation, did not lead to negative effects on native macro-arthropods. Although
496 this result does not match the general expectation (review in Spafford et al. 2013), it is

497 interesting to note that it is in agreement with the only published comparative study on the effect
498 of non-native plants on invertebrates at the community scale, and in the context of sub-Antarctic
499 islands (Gremmen et al. 1998). In this study, which focussed on soil fauna communities, native
500 macro-invertebrate abundance was similar or higher in vegetation dominated by the non-native
501 grass *Agrostis stolonifera* compared to vegetation dominated by *A. magellanica*. Obviously,
502 non-native plants would have had a negative impact on specialist native macro-arthropods
503 feeding on some particular native plant species. However, highly specialist native macro-
504 arthropods were scarce in our study, probably because we focussed on herbaceous habitats,
505 while specialist species were more likely to be found in fellfield habitats (Hullé and Vernon
506 2021). Two hypotheses may explain the lack of negative effects of non-native plants on native
507 macro-arthropods. First, the spatial scale of our paired sampling design, i.e., the short distances
508 separating native and non-native patches could result in native macro-arthropod communities
509 being composed of the same species in both types of patch. Indeed, the mosaic landscape and
510 entangled patterns of native and non-native plant communities observed on the islands studied
511 (Fig. 2) may allow between-patch movements of individuals either actively walking, or flying,
512 depending on species dispersal abilities, or passively carried by wind from and to nearby areas
513 (Schooley and Wiens 2003). At the scale of the patch, higher abundances of some macro-
514 arthropod species in non-native patches may be related to better local conditions provided by
515 the non-native plants. Similar small-scale distribution patterns in arthropods depending on plant
516 species within the vegetation mosaic have been described (e.g., Coulson et al. 2003). A second
517 hypothesis is that interactions between non-native and native macro-arthropods play a greater
518 role than plant-arthropod interactions in shaping native macro-arthropods. Indeed, an important
519 feature of macro-arthropod communities was that non-native species outnumbered native in
520 both types of vegetation, as already highlighted on Kerguelen archipelago (Frenot et al. 2005).
521 For instance, the predatory beetle *M. soledadinus* had a strong impact on native invertebrates

522 e.g., the flies *Anatalanta aptera* and *C. moseleyi*, resulting in their local extinction on some
523 coastal habitats of the Kerguelen Islands (Lebouvier et al. 2020). In our surveys, *M. soledadinus*
524 were few and could not have any impact on native arthropods. Dominant non-native taxa in our
525 study were the aphids, which are sap-feeders and the thrips *A. apteris*, which feeds on the
526 content of leaf cells (Karban and Strass 1994). By occupying previously vacant or unsaturated
527 ecological niche (Russel et al. 2017; Houghton et al. 2019), they probably don't compete with
528 native species. Since data is missing from locations on Kerguelen Islands that do not host non-
529 native invertebrates (Hullé and Vernon 2021) against which to compare the diversity and
530 abundance observed in our surveys, it is difficult to conclude on this hypothesis.

531

532 THE ABUNDANCE OF MACRO-ARTHROPODS OF DIFFERENT TROPHIC GROUPS IS 533 HIGHER IN NON-NATIVE VEGETATION

534 Non-native plants also had no negative effect on macro-arthropods belonging to different
535 trophic groups, i.e., herbivores, decomposers and predators whose diversity and abundance
536 were similar or higher in non-native patches. The aphid *M. ascalonicus* and the thrips *A. apteris*
537 much dominated among herbivores. Both species being polyphagous, they were able to feed on
538 native and non-native species such as *A. magellanica* and *T. gr ruderalia* (Karban and Strauss
539 1994; Hullé et al. 2003). Plant *FDIs* had an important contribution to explaining the abundance
540 of macro-herbivores, which benefited as expected from diversified resources (Carmona et al.
541 2011; Moretti et al. 2013). This result highlights that the traits we selected were involved in
542 herbivore-plant interactions, as also suggested by the strong positive effects of CWM_{SLA} and
543 CWM_{LL} on herbivore abundance. Decomposers mainly comprised omnivorous taxa, which feed
544 mostly on carcasses or faeces of mammals and seabirds. Their weak trophic link with plants
545 might explain their moderate response to native and non-native vegetation, as well as to plant
546 *FDIs*. Predator diversity and abundance were not impacted by plant *FDIs*. Predators, i.e., three

547 spiders, were more abundant in non-native patches relative to native, perhaps partly due to
548 differences in prey availability, which is an important factor driving spider dynamics (Pearson
549 2009). Indeed, these species have a very large diet consisting mainly of small insects (larvae,
550 adults) (Ysnel and Ledoux 1988), whose abundances were higher on non-native patches. This
551 result may contribute to explain higher abundances of native macro-arthropods in non-native
552 patches since the native spiders, *N. antarcticus* and *M. kerguelensis*, represented ~90% of their
553 abundance.

554

555 THE ABUNDANCE OF MICRO-ARTHROPODS IS LOWER IN NON-NATIVE 556 VEGETATION

557 Non-native plants had negative effects on the abundance of both Oribatida mites and
558 Symphypleona springtails. This result was also observed at *Marion Island* where
559 Symphypleona springtails and one dominant Oribatida species had higher abundances on the
560 native plant species *A. magellanica* than on the non-native *A. stolonifera* (Gremmen et al. 1998).
561 Several studies conducted in the sub-Antarctic islands, concluded that both mites and springtails
562 were mainly controlled by abiotic factors, in particular plant or soil moisture and temperature
563 (Travé 1981; McGeoch et al. 2006). Local plant community can have indirect effects on micro-
564 arthropods through the effects of plant traits on local abiotic conditions, which in turn may
565 affect micro-arthropods. For instance, such mechanisms were suggested to explain springtail
566 responses to different plant functional groups (Eisenhauer et al. 2011). In this study, lower
567 densities of springtails in the legume group were explained by higher plant biomass production,
568 which, by depleting soil water content, directly affected springtails; it also depleted nutrients in
569 the soil, which in turn negatively affected fungal growth, i.e., the amount of food available to
570 springtails. Interestingly, *FDis* had a strong negative effect on Symphypleona springtails and
571 no effect on Oribatida mites. These finding echoes that of Milcu et al. (2013) who found the

572 same results, and suggested that the negative effect of *FD* on springtail abundance was mediated
573 by its negative effect on root biomass. In contrast to macro-arthropods, micro-arthropods are
574 less mobile and therefore they might not be able to reach the native patches such as macro-
575 arthropods can do to find more resources. Further investigations on the relationship between
576 plants, soil micro-arthropods and their main food resources, i.e., soil microbes, could allow
577 understanding the mechanisms generating the results we observed. Indeed, we may hypothesize
578 that the negative effects of non-native plants on Oribatida mites and Symphypleona springtails
579 resulted at least partly from changes in the microbial networks in links to changes in plant
580 communities (Boeddinghaus et al. 2019; Karimi et al. 2019).

581

582 **CONCLUSION**

583 Our study contributes to document the under-explored question of the interactions between
584 plants and arthropods, in the context of biological invasions in the sub-Antarctic islands. This
585 is particularly true for micro-arthropods, where the drivers of community assemblages, inter-
586 specific interactions, species feeding preferences and ecology are largely unknown (Houghton
587 et al. 2019). Our results point out the importance of conducting studies at different spatial scales
588 and repeated over time, which could allow understanding the mechanisms by which non-native
589 plants change native communities and modify the dynamics of both plant and arthropod
590 communities. This would also make it possible to assess the long-term consequences for species
591 conservation and ecosystem functioning. Indeed, by changing abundances of macro-arthropods
592 belonging to different trophic groups and by depleting micro-arthropods, which are essential
593 for nutrient cycling and primary production in terrestrial ecosystems, our findings suggest that
594 non-native plant species may alter trophic interactions and whole ecosystem functioning in sub-
595 Antarctic islands.

596

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800

801 **Table 1.** Effect of island, type of plant patch (native or non-native) and their two-way interaction on the plant community functional diversity
802 (FD_{is}) and the community-weighted means of plant traits (CWM_{TRAIT}). CWM_{PH} = plant height, CWM_{PW} = plant width, CWM_{LL} = leaf length, CWM_{LA}
803 = leaf area, CWM_{LT} = leaf thickness, CWM_{SLA} = specific leaf area, CWM_{LDMC} = leaf dry matter content. Values and significance of Type II Wald
804 Chi-square tests, χ^2 , realized on fixed effects tested in LMM models (Island: χ^2_2 Type of patch: χ^2_1 , Island \times Type of patch: χ^2_2). Significant fixed
805 effects are in bold. We also show predicted means \pm standard errors ($\alpha = 0.05$) of FD_{is} and CWM_{TRAIT} 's for each island \times type of patch combination.
806

| Variable | Fixed factor | χ^2 | $p (>\chi^2)$ | <i>Île Australia</i> | | <i>Île aux cochons</i> | | <i>Île Mayes</i> | |
|-----------------|-------------------------------|----------|--------------------|----------------------|-------------------|------------------------|-------------------|-------------------|-------------------|
| | | | | Native patch | Non-native patch | Native patch | Non-native patch | Native patch | Non-native patch |
| FD_{is} | Island | 9.16 | 0.0103 | | | | | | |
| | Type of patch | 1.47 | 0.2258 | 0.081 \pm 0.023 | 0.081 \pm 0.023 | 0.158 \pm 0.023 | 0.158 \pm 0.023 | 0.155 \pm 0.023 | 0.155 \pm 0.023 |
| | Island \times Type of patch | 1.28 | 0.5255 | | | | | | |
| CWM_{PH} (cm) | Island | 235.34 | < 0.0001 | | | | | | |
| | Type of patch | 117.88 | < 0.0001 | 16.8 \pm 0.9 | 23.9 \pm 0.9 | 21.5 \pm 0.9 | 25.2 \pm 0.9 | 25.3 \pm 0.9 | 35.5 \pm 0.9 |
| | Island \times Type of patch | 34.62 | < 0.0001 | | | | | | |
| CWM_{PW} (cm) | Island | 6.36 | 0.0416 | | | | | | |
| | Type of patch | 10.18 | 0.0014 | 15.4 \pm 1.8 | 20.7 \pm 1.8 | 11.7 \pm 1.8 | 17.1 \pm 1.8 | 16.8 \pm 1.8 | 22.2 \pm 1.8 |
| | Island \times Type of patch | 0.58 | 0.7479 | | | | | | |

| | | | | | | | | | |
|---|-------------------------------|--------|-----------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| CWM_{LL} (cm) | Island | 12.30 | 0.0021 | | | | | | |
| | Type of patch | 92.30 | < 0.0001 | 7.3 ± 1.0 | 16.0 ± 1.6 | 8.9 ± 1.2 | 18.4 ± 1.7 | 12.3 ± 1.4 | 23.1 ± 1.9 |
| | Island \times Type of patch | 1.83 | 0.3997 | | | | | | |
| CWM_{LA} (cm ²) | Island | 6.45 | 0.0396 | | | | | | |
| | Type of patch | 9.78 | 0.0017 | 16.8 ± 6.4 | 31.9 ± 8.8 | 12.7 ± 5.6 | 26.1 ± 8.0 | 34.0 ± 9.1 | 54.3 ± 11.5 |
| | Island \times Type of patch | 1.33 | 0.5131 | | | | | | |
| CWM_{LT} (mm) | Island | 14.36 | 0.0008 | | | | | | |
| | Type of patch | 224.60 | < 0.0001 | 0.69 ± 0.03 | 0.38 ± 0.02 | 0.60 ± 0.03 | 0.33 ± 0.02 | 0.74 ± 0.04 | 0.41 ± 0.02 |
| | Island \times Type of patch | 5.5 | 0.0638 | | | | | | |
| CWM_{SLA} (cm ² g ⁻¹) | Island | 2.70 | 0.2589 | | | | | | |
| | Type of patch | 82.4 | < 0.0001 | 139.0 ± 4.5 | 192.0 ± 4.5 | 139.0 ± 4.5 | 192.0 ± 4.5 | 139.0 ± 4.5 | 192.0 ± 4.5 |
| | Island \times Type of patch | 0.18 | 0.9142 | | | | | | |
| CWM_{LDMC} | Island | 12.02 | 0.0024 | | | | | | |
| | Type of patch | 7.04 | 0.0079 | 0.255 ± 0.015 | 0.224 ± 0.015 | 0.287 ± 0.015 | 0.256 ± 0.015 | 0.225 ± 0.015 | 0.194 ± 0.015 |
| | Island \times Type of patch | 1.40 | 0.4945 | | | | | | |

807

808

809 **Table 2.** Effect of island, type of patch (native or non-native), their two-way interaction and plant community *FDis* on macro-arthropod taxa
810 richness and abundance, and micro-arthropod abundance. Taxa richness was calculated pooling pitfall traps and yellow pans. Taxa abundance was
811 calculated using pitfall trap data (macro-arthropods: native species, predators; micro-arthropods) or yellow pan data (macro-arthropods: herbivores,
812 decomposers). Values and significance of Type II Wald Chi-square tests, χ^2 , realized on all fixed effects tested in GLMM (native macro-arthropod
813 abundance, Symphypleona abundance) or LMM (all other models). Significant fixed effects in the simplified models are in bold.

| Arthropod taxa and metrics | Island | | Type of patch | | Island \times Type of patch | | <i>FDis</i> | |
|----------------------------|----------|-------------------|---------------|-------------------|-------------------------------|---------------|-------------|---------------|
| | χ^2 | $p (>\chi^2)$ | χ^2 | $p (>\chi^2)$ | χ^2 | $p (>\chi^2)$ | χ^2 | $p (>\chi^2)$ |
| Macro-arthropod richness | | | | | | | | |
| Native species | 11.58 | 0.0030 | 0.36 | 0.5456 | 5.63 | 0.0597 | 5.63 | 0.0175 |
| Non-native taxa | 17.76 | 0.0001 | 1.03 | 0.3103 | 4.45 | 0.1081 | 1.29 | 0.2560 |
| All taxa | 24.99 | <0.0001 | 5.24 | 0.0220 | 16.52 | 0.0003 | 8.91 | 0.0028 |
| Decomposers | 10.98 | 0.0041 | 0.61 | 0.4337 | 9.60 | 0.0082 | 3.01 | 0.0824 |
| Predators | 4.11 | 0.1281 | 0.52 | 0.4702 | 8.52 | 0.0141 | 1.07 | 0.3000 |
| Macro-arthropod abundance | | | | | | | | |
| Native species | 19.38 | <0.0001 | 29.98 | <0.0001 | 5.17 | 0.0751 | 2.53 | 0.1113 |
| Herbivores | 0.65 | 0.7206 | 25.55 | <0.0001 | 11.93 | 0.0025 | 13.03 | 0.0003 |
| Decomposers | 12.28 | 0.0021 | 1.29 | 0.2549 | 7.32 | 0.0256 | 0.11 | 0.7387 |
| Predators | 21.17 | <0.0001 | 11.08 | 0.0009 | 6.78 | 0.0337 | 1.51 | 0.2184 |
| Micro-arthropod abundance | | | | | | | | |
| Oribatida mites | 4.09 | 0.1294 | 5.57 | 0.0183 | 0.75 | 0.6870 | 0.039 | 0.8423 |

814

| | | | | | | | | |
|-------------------------|-------|---------------|-------|-------------------|------|--------|-------|-------------------|
| Symphyleona springtails | 12.58 | 0.0019 | 79.63 | <0.0001 | 2.83 | 0.2423 | 41.35 | <0.0001 |
|-------------------------|-------|---------------|-------|-------------------|------|--------|-------|-------------------|

815 **FIGURE CAPTIONS**

816 **Fig. 1** Map of Kerguelen Islands and location of Kerguelen Islands in the Southern Indian
817 Ocean

818

819 **Fig. 2** Vegetation maps, based on Pléiades 1A PMS satellite image acquired in 2016, in 1 km²
820 areas around the sampled patches, and location of the sampled patches (centroids) within native
821 and non-native areas. Native patches are in white and non-native patches in black and white.
822 Vegetation was classified in 10 classes: Steppe dominated by non-native Poaceae; Tall grassland
823 of non-native Poaceae; Mixed herbfield of native and non-native species; Tall herbfield of
824 *Acæna magellanica* (ACAMA); Tundra of *Azorella selago* (AZOSE), *A. magellanica* and
825 *Festuca contracta* (FESCO); Native herbfield of *A. selago*, *A. magellanica* and *Pringlea*
826 *antiscorbutica* (PRIAN); Open cushion-carpet of *A. selago*; Mire; Steppe dominated by native
827 Poaceae; Fellfield. See Online Resource 1 for a detailed description of the classes. Maps
828 highlight spatial patterns of vegetation, contrasting vegetation dominated by native plant
829 species (in green) and vegetation dominated by non-native plants species (in yellow and pink)

830

831 **Fig. 3** Mean plant species cover over the five quadrats per patch, in native and non-native
832 patches in the islands studied: *Île Australia* (a) native patches (d) non-native patches, *Île aux*
833 *Cochons* (b) native patches (e) non-native patches, *Île Mayes* (c) native patches (f) non-native
834 patches). Native plant species: *Acaena magellanica* (ACAMA), *Azorella selago* (AZOSE),
835 *Deschampsia antarctica* (DESAN), *Festuca contracta* (FESCO), *Galium antarcticum*
836 (GALAN), *Ranunculus biternatus* (RANBI), *Pringlea antiscorbutica* (PRIAN); Non-native
837 plant species: *Cerastium fontanum* (CERFO), *Cerastium glomeratum* (CERGL), *Poa annua*
838 (POAAN), *Poa pratensis* (POAPR), *Sagina procumbens* (SAGPR), *Stellaria alsine* (STEAL),

839 *Stellaria media* (STEME), *Taraxacum erythrospermum* (TARER), *Taraxacum gr. ruderalia*
840 (TAROF), *Vulpia bromoides* (VULBR)

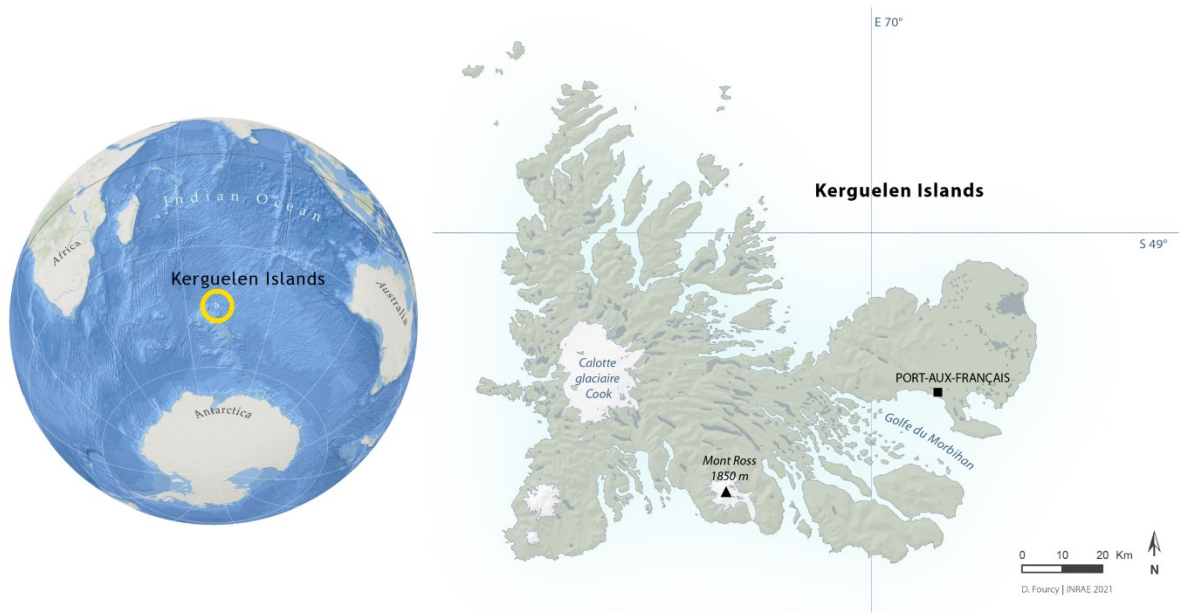
841

842 **Fig. 4** Model predictions $\pm SE$ of the effect of the type of patch (native in green, non-native in
843 red) on macro-arthropod abundance: (a) native species (pitfall traps) (see Table 2 for GLMM
844 results), (b) herbivores (yellow pan counts), (c) decomposers (yellow pan counts) and (d)
845 predators (pitfall trap counts) (see Table 2 for LMM results). Predictions are on a log scale.
846 Shown are the results of the comparison between native and non-native patches (additive effect:
847 p is the p -value of Chi-square test, χ^2 in LMM or GLMM; interactive effect with the island: p
848 is the p -value for comparing the estimates of native vs non-native patches within each island
849 with Tukey's method and paired contrasts)

850

851 **Fig. 5** Model predictions $\pm SE$ of the effect of the type of patch (native in green, non-native in
852 red) on micro-arthropod abundance: (a) Oribatida mites (pitfall trap) (see Table 2 for LMM
853 results), and (b) Symphypleona springtails (pitfall traps) (see Table 2 for GLMM results).
854 Predictions are on a log scale. Shown are the results of the comparison between native and non-
855 native patches (additive effect: p is the p -value of Chi-square test, χ^2 in LMM or GLMM)

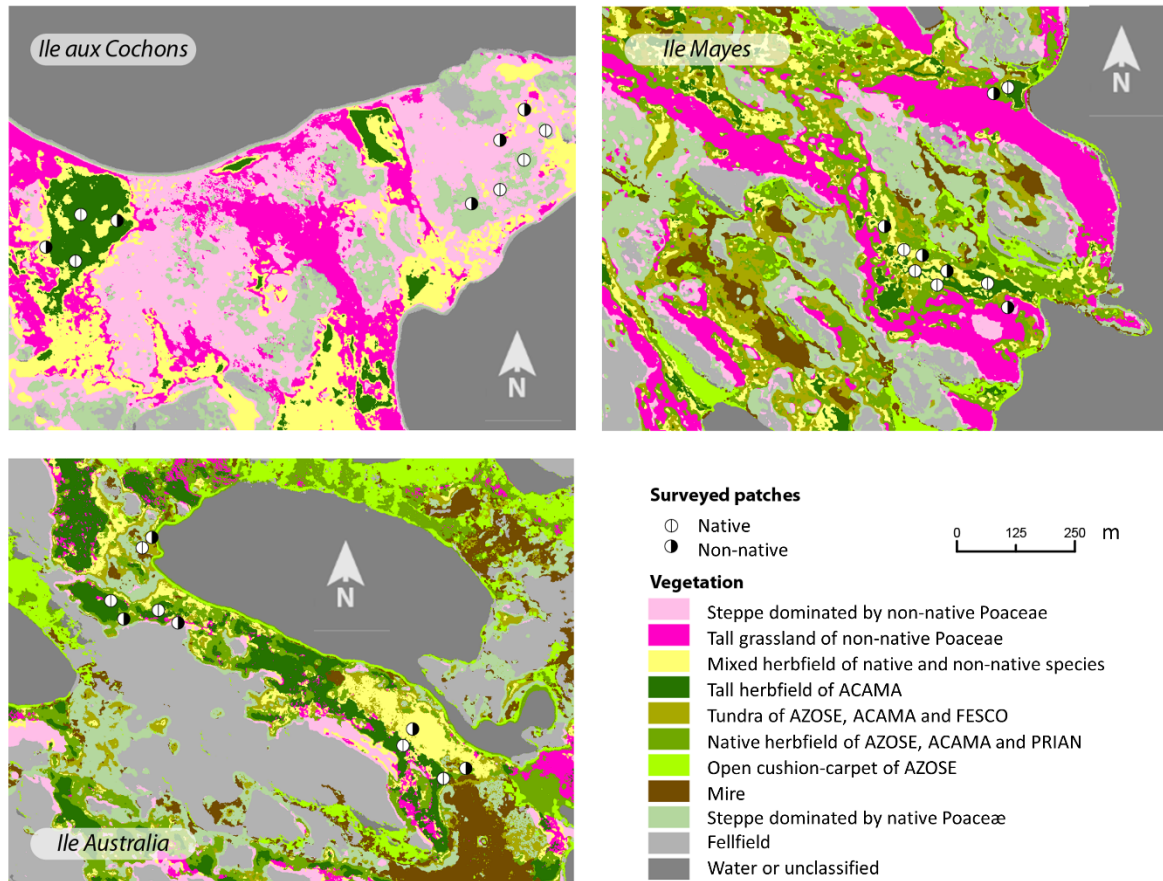
856



857

858 Fig. 1

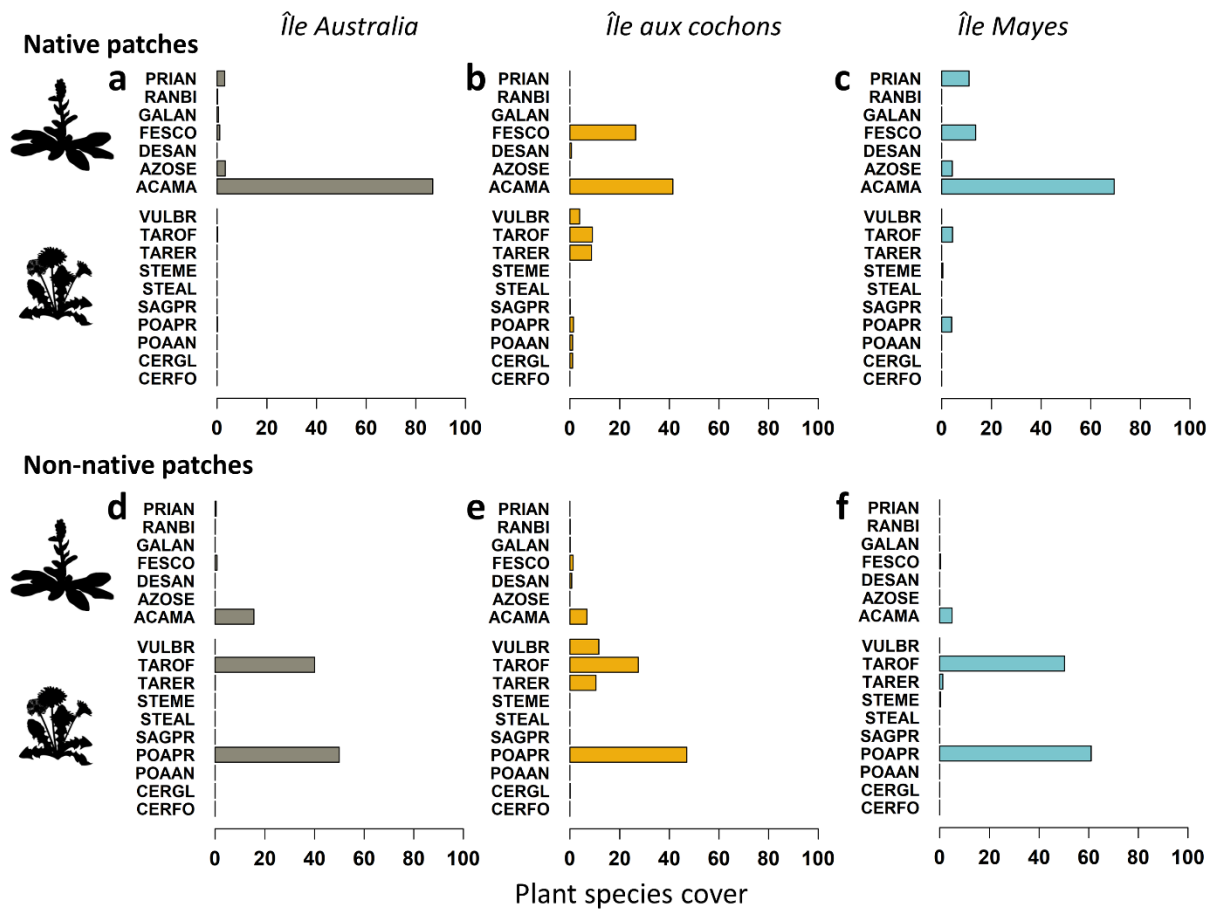
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860

861 Fig. 2

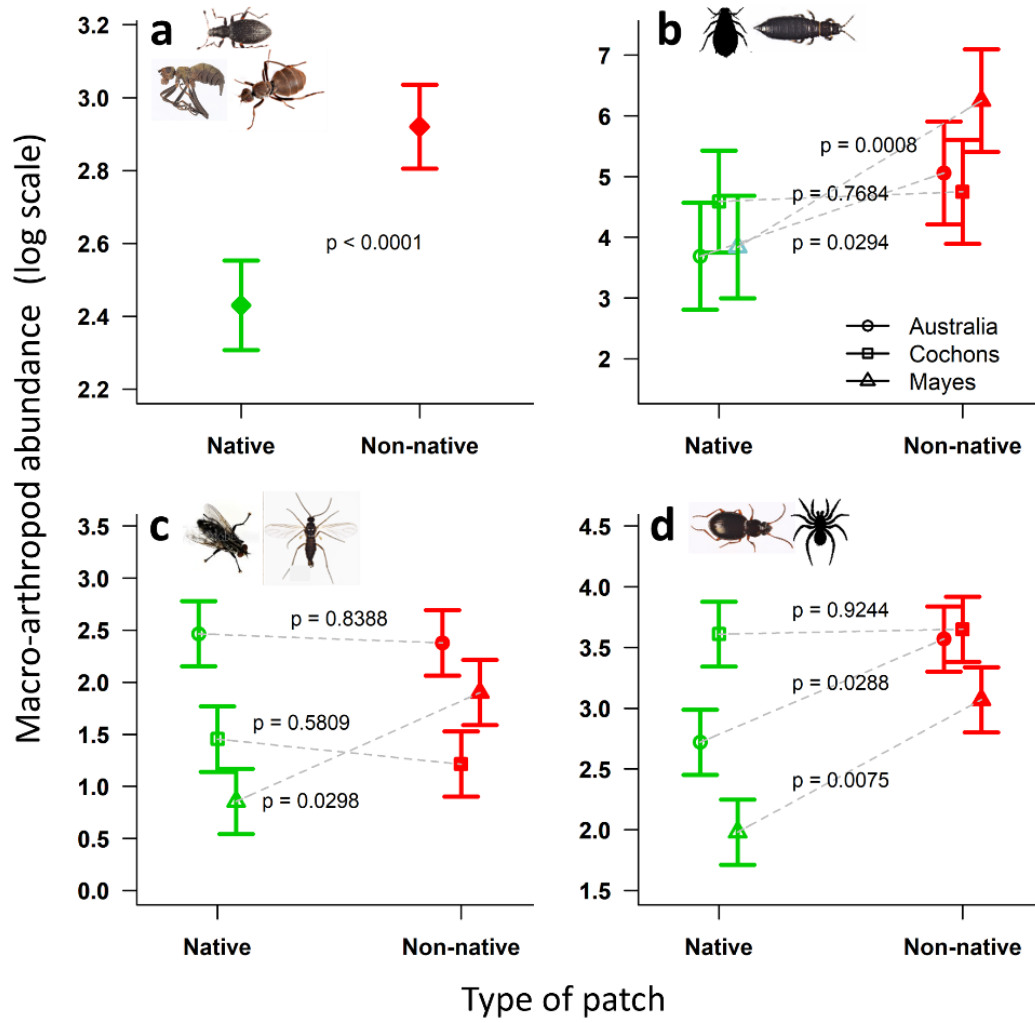
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864 Fig. 3

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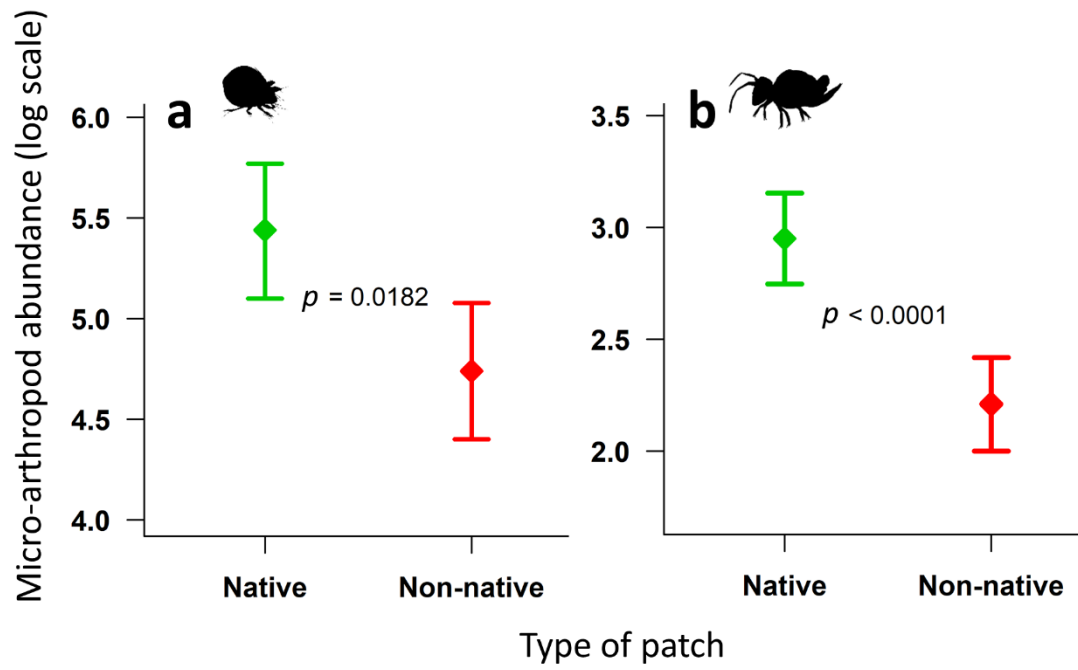


866

867 Fig. 4

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870

871 Fig. 5

872

873 **Supplementary Information**

874 Additional Supporting information may be found in the online version of this article:

875 **Online resource 1.** Description of vegetation categories used to map vegetation on the three
876 islands studied

877 **Online resource 2.** Physical description of the surveyed vegetation patches

878 **Online resource 3.** PCA results conducted on CWM_{TRAITs} (community-weighted means of
879 plant trait) calculated on native and non-native vegetation patches. PH = plant height, PW=plant
880 width, LL=leaf length, LA=leaf area, LDMC=leaf dry matter content, SLA=specific leaf area,
881 LT=leaf thickness

882 **Online resource 4.** Results and model outputs of the comparison between patch model and
883 single CWM_{TRAIT} models

884 **Online resource 5.** Cumulated counts of three macro-arthropod trophic groups: herbivores,
885 decomposers and predators, collected in pitfall traps and in yellow pans, on the three islands
886 studied (*Île Australia* in grey, *Île aux Cochons* on yellow, *Île Mayes* in blue) in non-native (in
887 red) and native patches (in green)